

PARALVINELLA GRASSLEI, NEW GENUS, NEW SPECIES
OF ALVINELLINAE (POLYCHAETA: AMPHARETIDAE)
FROM THE GALÁPAGOS RIFT GEOTHERMAL VENTS

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Abstract.—Several unknown or newly described animals forming a flourishing community, have been collected in the immediate vicinity of the warm hydrothermal springs east of the Galápagos Islands. Among them, a polychaetous annelid collected within the tubemass of vestimentiferan worms represents a new genus and species, *Paralvinella grasslei*, placed in the subfamily Alvinellinae, recently erected within the family Ampharetidae for *Alvinella pompejana* Desbruyères and Laubier, 1980, a species collected at another hydrothermal area on the East Pacific Rise at 21°N. *Paralvinella grasslei* exhibits fewer morphological and biological adaptations than *A. pompejana*. The two species are compared. It is suggested that they originated from a single ancestral population that became divided into isolated subpopulations.

One of the major biological discoveries of the last decade is the rich and unusual fauna clustered around thermal springs at centers of rapid seafloor spreading, at depths from 2500 to 2700 meters. The thermal springs were first discovered on the Galápagos Rift in February 1977, using the research submersible Alvin (Ballard 1977). Early in 1979, more geothermal vents were discovered west of the original area, as well as further north along the East Pacific Rise spreading zone near the Mexican coast at latitude 21°N. All active vents were found to be surrounded by very dense populations of benthic animals, such as mussels, present only on the Galápagos Rift, clams, and vestimentiferan tubeworms of unusually large size (Galápagos Biology Expedition Participants 1979).

In a recent paper (Desbruyères and Laubier 1980), we described a new genus and species of tubicolous polychaete collected during the RISE cruise of the research submersible Alvin (April–May 1979) on the East Pacific Rise at 21°N. In spite of several aberrant features, the polychaete, named *Alvinella pompejana*, was placed in the family Ampharetidae (order Terebellida) and in a new subfamily, Alvinellinae, which exhibits remarkable biological features, in particular the existence of two successive ontogenetic states.

Alvinella pompejana, very abundant at the East Pacific Rise vents, has not been observed at the Galápagos Rift vents, although some species such as the clam *Calyptogena magnifica* Boss and Turner, 1980, the crab *Bythograea thermydron* Williams, 1980, and the vestimentiferan tubeworm *Riftia pachyptila* Jones, 1981, are common in both hydrothermal areas. From a biogeographical point of view it can be emphasized that these unusual species belong basically to the same faunal pool and derive from a single evolutionary trend.

While the description of *Alvinella pompejana* was in press, we received from Dr. Frederik Grassle a single specimen of Alvinellinae found among washings from vestimentiferan worms at the “Rose Garden” site, Galápagos Rift. Sur-

prisingly, this new species differs markedly from *A. pompejana*. According to the generic features usually recognized within the Ampharetidae, these differences clearly merit the erection of a second genus within Alvinellinae. Even though it might be considered somewhat injudicious to create a new genus and species based on a single specimen, the biogeographical and evolutionary aspects of this unexpected discovery are considered sufficiently important to justify a preliminary description. While this paper was being reviewed, a second specimen from the same station was found by Dr. Meredith L. Jones in a vestimentiferan tube, confirming our first conclusions.

Order: Terebellida

Family: Ampharetidae Malmgren, 1865

Subfamily: Alvinellinae Desbruyères and Laubier, 1980

Paralvinella, new genus

Type-species.—*Paralvinella grasslei*.

Etymology.—Derived from the generic name *Alvinella* which is dedicated to the Alvin team.

Diagnosis.—Body long and posteriorly attenuated. Prostomium extremely reduced, lacking appendages. Numerous smooth oral tentacles invaginable in buccal cavity, together with paired ventral structures. Body with 2 indistinct regions separated only by slight decrease in diameter; thoracic or abdominal regions not characterized by definite structures. Four pairs of branchiae on 4 segments, first achaetous, last 3 setigerous. Paleae absent. Setigerous segment 7 modified, with large prominent acicular hooks. Some anterior notopodia with digitiform dorsal lobe. Notosetae capillary and smooth when viewed with light microscope. Sessile uncinigerous tori starting on setiger 15 and continuing posteriorly. Uncini arranged in single rows, each with only 2 unequal teeth. Pygidium rounded, without appendages.

The main characteristic features of *Paralvinella* agree well with the diagnosis of the subfamily Alvinellinae: first segment achaetous with branchiae, one anterior segment modified, parapodia normally biramous, with capillary notosetae and uncinigerous neuropodial tori. However, presence of ventral paired structures in the buccal apparatus would lead to a slight change in the subfamily definition. It seems premature to propose an emended diagnosis at the moment.

Paralvinella grasslei, new species

Figs. 1, 2

Type-locality, material examined.—Two specimens collected during Alvin dive 990, 7 December 1979, Galápagos Rift, "Rose Garden" area, 2451 meters depth, 00°48'25"N, 86°13'48"W. Holotype found among washings of vestimentiferan tubes, second specimen recovered in empty tube of a young adult *Riftia*. Holotype deposited in the collections of the Division of Worms, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 67703).

Etymology.—This species is named for Dr. Frederik Grassle, Woods Hole Oceanographic Institution, Chief Scientist of the Galápagos Biology Expedition.

Description.—Holotype 43 mm in length and 4.8 mm in greatest width (anterior

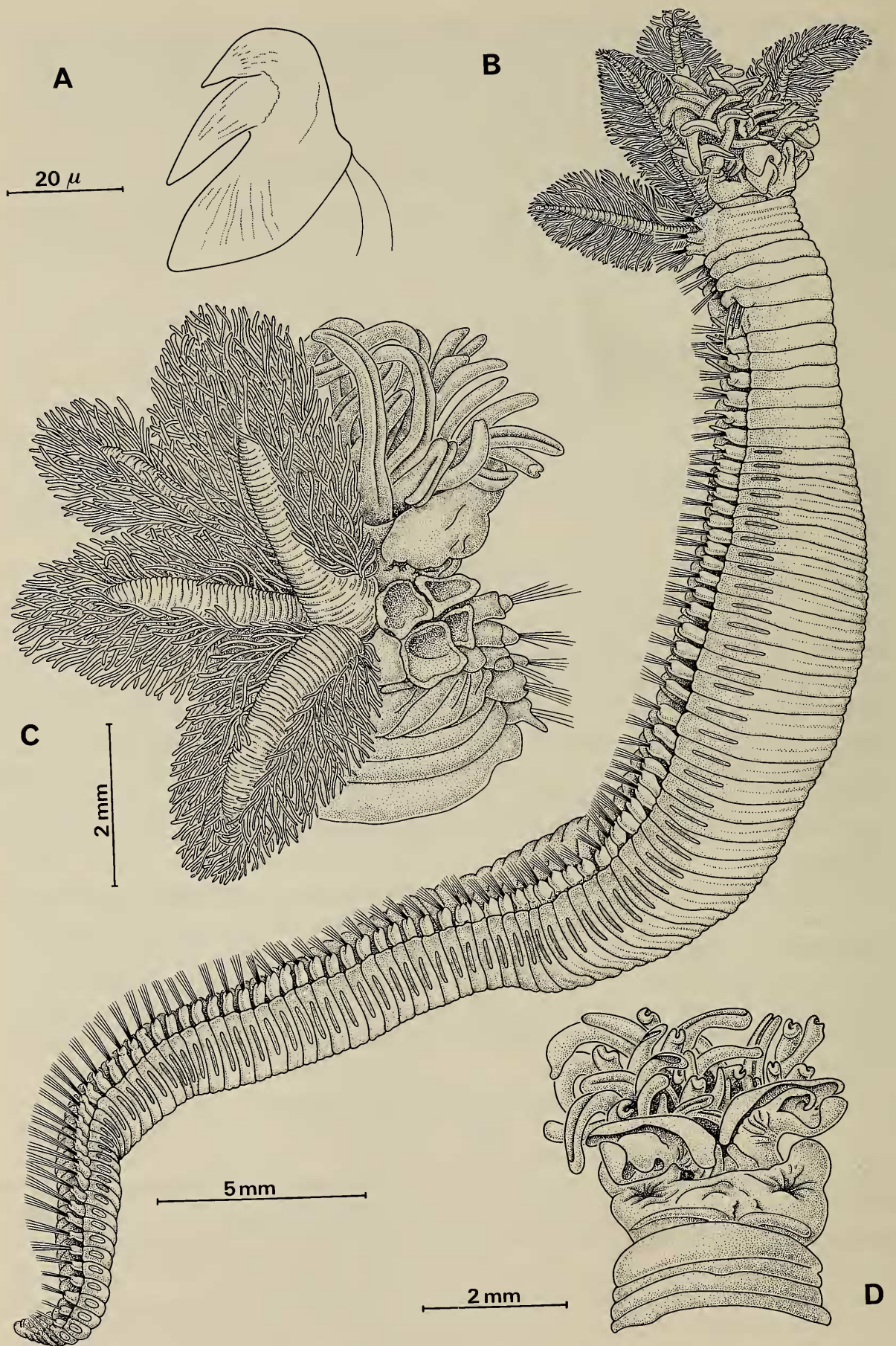


Fig. 1. *Paralvinella grasslei*: A, Uncinus in lateral view; B, Habitus in latero-ventral view with oral tentacles extended; C, Anterior end in dorsal view, right branchiae removed; D, Anterior end in ventral view, showing paired structures and oral tentacles.

third), with 99 setigerous segments. Second specimen 54 mm in length and 4 mm wide, with 104 setigerous segments. Color after preservation in ethanol pinkish, slightly iridescent, with normal and modified setae bright yellow. Body comprises large anterior part, followed by decrease in diameter between setigers 47 to 52, posterior part slender and tapering to pygidium (Fig. 1B). No ventral shields.

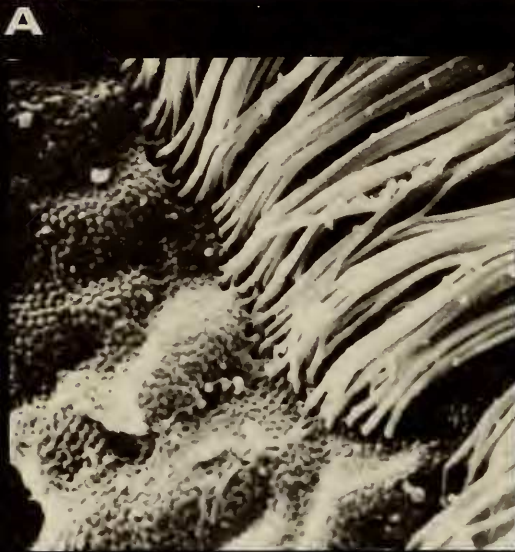
Prostomium extremely reduced, devoid of glandular ridges or ocular patches, completely hidden by branchiae. Peristomium with 2 large lateral lobes enclosing prostomium laterally, and ventral lip bearing paired lateral hollows and paired transverse glandular crests (Fig. 1D). Buccal apparatus comprising large number of smooth oral tentacles, each with marked ciliated groove along one side, and two ventral paired structures, each arising from single short median stem, ending in 3 rounded lobes (Fig. 1D). (It was not possible, without greatly damaging the animals, to elucidate the insertion of the oral tentacles and paired structures, nor to confirm the morphology of the prostomium.)

First segment achaetous, clearly separated from cephalic region and fused dorsally with next 3 setigerous segments; faint transverse lines ventrally. Next 3 setigerous segments with paradodia reduced to notopodia with capillary setae disposed in latero-dorsal line. Branchial region formed by first 4 segments with 4 pairs of branchiae, together with dorsal part of slightly expanded fifth segment. Branchiae all similar, strong and regularly attenuated, stem with large number of slender filaments irregularly inserted on 2 opposite narrow areas of stem (Figs. 1B, C; 2A, C). Branchial filaments with 2 opposed lines of small pores, $0.10\ \mu\text{m}$ in diameter with long, slender secondary filaments arising from them. Morphological detail same as in branchial lamellae of *Alvinella pompejana*.

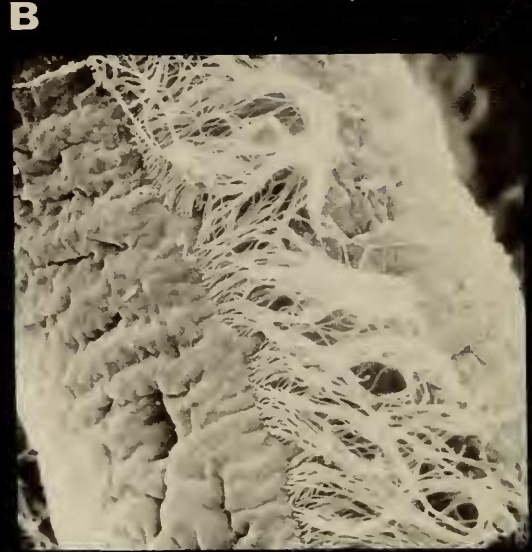
Next 11 segments (segments 5 to 15, setigers 4 to 14) also with parapodia reduced to notopodia (except the modified segment). Posterior segments (from segment 16 or setiger 15) with notopodia and neuropodia with single rows of uncini. Setigers 6 to 15 with dorsal digitiform lobe on notopodium increasing in size from setiger 6 to maximum on setigers 10–13, then decreasing (Fig. 1B). Segment 8 (setiger 7) strongly modified, lacking notopodium. On right side of holotype, neuropodium with 3 very large acicular hooks directed posteriorly; no hooks at all on left side but empty socket is clearly visible (probably damaged). On left side of paratype neuropodium with 4 very large acicular hooks directed posteriorly; no hooks visible on right side but they can be seen internally using X-radiography. Following segment not modified. Notopodia of anterior unmodified segments well developed, provided with 10 to 15 capillary notosetae per notopodium. Notosetae covered with continuous layer of minute spinelets when viewed under scanning electron microscope (Fig. 2D). In cross section, notosetae with regular network of hexagonal fibers $0.5\ \mu\text{m}$ in diameter with median cylindrical canal.

From segment 16 (setiger 15), uncinigerous neuropodial tori present and continuing to end of body, without developing pinnules. Number of uncini per row 25–45, in single rows, with teeth facing anteriorly (retrogressive situation). Uncini with one main tooth surmounted by smaller secondary tooth (Fig. 1A), as in *A. pompejana*.

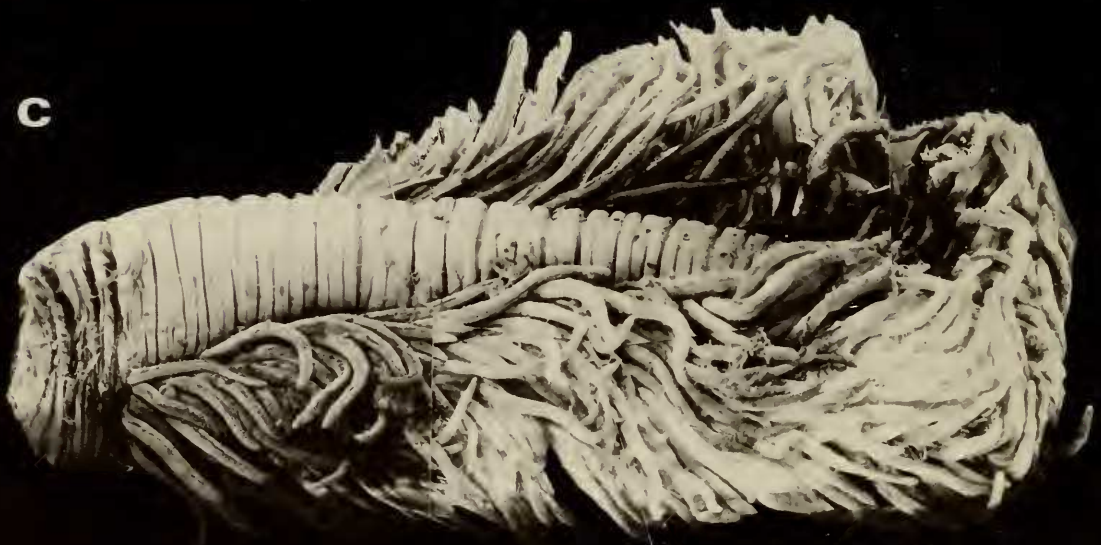
From segments 48 to 53, body diameter decreasing abruptly from 4.8 mm to 2.7 mm, with no other morphologically distinctive features. Pygidium rounded, lacking appendages, with anus opening in center.



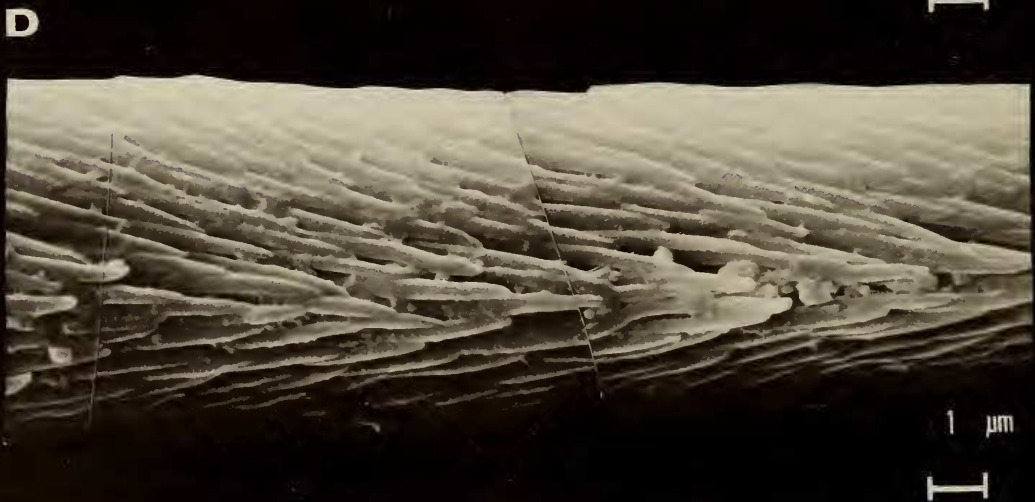
1 μ m



5 μ m



200 μ m



1 μ m



Ethology and ecology.—The 2 specimens were found without parchment-like tubes; the holotype was found among washings of vestimentiferan tubes, the second specimen was recovered from the empty tube of a young adult *Riftia*. Both come from the same dive on the “Rose Garden.” The “Rose Garden” geothermal vent area is characterized by dense beds of the vestimentiferan *Riftia pachyptila* Jones, 1981, living near geothermal vents from which flow warm water at 15° to 20°C, and probably using internal symbiotic bacteria and/or their metabolites as a source of organic carbon. Compared with *Alvinella pompejana*, *Paralvinella grasslei* shows no morphological adaptations which might be related to the uptake of dissolved organic material. From several measurements of temperature at the Galápagos Rift areas, a temperature of 20°C seems to be the highest to which *P. grasslei* is exposed; on the contrary, colonies of *Alvinella pompejana* seem to be restricted to waters with temperatures ranging upward from 30°C. *Alvinella pompejana* is probably adapted to peculiar ecological conditions that do not occur at the Galápagos Rift.

Comparison of *P. grasslei* and *A. pompejana*

For the following reasons *P. grasslei* is comparable to the juvenile of *A. pompejana*: they both show body constrictions at about the same distance from the anterior end, from segments 49 to 54 in *A. pompejana*, and from segments 48 to 53 in *P. grasslei*; they both are only slightly attenuated in the posterior regions, in contrast to the abrupt tapering at the posterior end of the adult *A. pompejana*. This conclusion does not imply the existence of a different adult form for *P. grasslei*. However, there are some arguments against the existence of a comparable juvenile form in *P. grasslei*: the posterior part of *P. grasslei* does not show any modification comparable to the notopodial extensions and their ciliated tips in the case of the juveniles of *A. pompejana*; also, there is nothing comparable in *P. grasslei* to the necrotic dorsal area of the constricted region of *A. pompejana*. In fact, it seems highly probable that there is only one form in *P. grasslei*, and that this form is not a juvenile of the sort found in *A. pompejana*.

Apart from this biological comparison, which does not alone justify the erection of a new genus, the 2 species differ as follows: there is a lobate buccal structure, in addition to the oral tentacles, in *P. grasslei*; the prostomium is extremely reduced in *P. grasslei*; the peristomium is well-developed, with 2 lateral expansions, in *P. grasslei*; there are filamentous branchiae in *P. grasslei*, lamellate branchiae in *A. pompejana*; the branchial region is composed of 4 segments, the first achaetous and the next 3 setigerous in *P. grasslei*, and of one achaetous segment only in *A. pompejana*; there is a single modified anterior segment with acicular setae in *P. grasslei* (segment 8), while there are 2 in *A. pompejana* forming a more complex system (segments 5 and 6); some anterior notopodia of *P. grasslei* bear digitiform dorsal lobes while such lobes are lacking in *A. pompejana*; the notosetae of the 2 species are of differing structure.

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Fig. 2. *Paralvinella grasslei*: A, B, Detailed and general view of branchial filament; C, Isolated branchia; D, Part of capillary notoseta. (Scanning electron micrographs)

Table 1.—Comparison of diagnostic characters of the two species of Alvinellinae.

	<i>Paralvinella grasslei</i>	<i>Alvinella pompejana</i>
Prostomium	Extremely reduced	Reduced
Peristomium	Well-developed, with 2 lateral expansions	Reduced
Buccal structures	Lobate paired structure with oral tentacles	Oral tentacles only
Branchial region	4 pairs of branchiae on 4 segments, first achaetous, three setigerous	4 pairs of branchiae on first achaetous segment
Type of branchiae	Filamentous	Lamellate
Modified segments with acicular hooks	Segment 8 (setiger 7)	Segments 5 and 6 (setigers and 4 and 5)
Anterior notopodia	With digitiform dorsal lobes	Digitiform notopodial lobes lacking
Posterior notopodia	Not modified	Complex ciliated digitiform notopodial extensions on juveniles
Dorsal part of segments	Not modified	Covered with dense tubular structures in adults
Ontogenetic stages	One ontogenetic stage only, corresponding to juvenile stage of <i>A. pompejana</i>	Two different ontogenetic stages, the juvenile stage with twice number of segments of adult stage
Notosetae	Capillary, smooth when viewed under light microscope	Capillary, geniculate, with 2 longitudinal rows of alternating teeth
Tube	Unknown	Parchment-like tube covered with particles of metallic sulfide
Occurrence and distribution	Among vestimentiferan tubes, Galápagos hydrothermal area, temperature 10 to 20°C	In spongy masses on hydrothermal vents, East Pacific Rise near 21°N, temperature at least 32°C

These various characters, compared with the conventional diagnostic features of the Ampharetidae, fully justify the erection of a new genus for the Galápagos Rift polychaete, and serve as well to reinforce the isolated position of the subfamily Alvinellinae within the family. The structure of the uncini with only 2 teeth in the Alvinellinae is not at all typical of the Ampharetidae, and is probably one of the more important characteristics of the aberrant Alvinellinae.

This comparison between *P. grasslei* and *A. pompejana* enables one to conclude that they are much closer to one another than to any other genus of Ampharetidae. The phylogenetic relationships between *P. grasslei* and *A. pompejana* can be elucidated from the structure of the branchial region and the position of the modified anterior segment. General trends of evolution in the Ampharetidae include reduction of branchial segments by the cephalization process (Day 1964):

in the primitive situation, there is one pair of branchiae on each branchial segment (ordinarily 4 branchial segments in the Ampharetidae). This process of cephalization could very well apply to *P. grasslei* and *A. pompejana*, assuming that the 4 distinct branchial segments of *P. grasslei* are fused to give the single achaetous segment in *A. pompejana*. Cephalization usually does not affect more posterior specific features, such as the position of modified segments.

This is clearly the case relative to *P. grasslei* (modified segment being segment 8) and *A. pompejana* (first modified segment being segment 5). This suggests the direction of the evolutionary relationship between the species, *P. grasslei* being more primitive than *A. pompejana*.

Taken as a whole the differences between the two species fully justify the erection of a new genus for the Galápagos polychaete (Table 1).

Apart from the systematic and phylogenetic relationships, another comparison must be made from a biological point of view, i.e., the feeding behavior and corresponding morphological adaptations. Like most Ampharetidae, *P. grasslei* is probably a surface deposit-feeder (Fauchald and Jumars 1979). It has oral tentacles as well as buccal structures; the latter are probably more efficient than the tentacles and enable the animal to catch larger particles. The situation is quite different for *A. pompejana*, which, in addition to the oral tentacles, has special tubular structures along the body of the adult; they can probably be considered as an adaptation for taking up released dissolved organic material (Desbruyères and Laubier 1980:272). It is impossible to estimate the importance of this uptake of dissolved organic material compared with surface deposit-feeding. Still, *A. pompejana* lives very close to high temperature hydrothermal vents, much closer than most other species of the hydrothermal community, the vestimentiferan *Riftia pachyptila* being the other species close to the vents. Organic material released by bacterial activity in the immediate vicinity of the vents could be an important trophic source for *A. pompejana*, but there is no evidence for this as yet. Suggestions that chemo-autotrophic bacteria present in the hydrothermal waters are a major food source for filter-feeding organisms such as the mytilid mussel from the Galápagos Rift hydrothermal area have been proposed (Rau and Hedges 1979). More recent data indicate that organic nitrogen of nutritional importance for vent animals is initially synthesized within the vent environment and this synthesis may be preceded by N₂ fixation (Rau 1981).

Biogeographical and Evolutionary Remarks

It is obviously difficult in the present stage of our knowledge to establish the evolutionary relationships between *P. grasslei* and *A. pompejana*: both are known from single and limited locations, and *P. grasslei* by 2 specimens only. The direct distance between the Galápagos Rift and the East Pacific Rise near 21°N, is approximately 1800 nautical miles. Following the axis of the Rift and Rise, where hydrothermal activity can occur, the distance is much greater, nearly 2200 nautical miles. Due to the relatively large size of both species of Alvinellinae and the recent progress in sampling deep-sea benthic organisms, there is very little doubt that they live only in the immediate vicinity of hydrothermal vents where a supply of organic matter is made available through chemo-autotrophy. Another pertinent argument is given by the discovery of large accumulations of dead giant clams

(*Calyptogena magnifica*) in areas of the East Pacific Rise, 21°N, where hydrothermal vents are no longer active (Francheteau *et al.* 1980:76–77). Those clam cemeteries associated with “dead” vent areas clearly demonstrate the basic role of hydrothermalism as the direct or indirect energy source of these animal communities (Enright *et al.* 1981).

Assuming that both species of Alvinellinae, as well as certain benthic organisms, are strictly linked with hydrothermal vents and bacterial chemo-autotrophy, one has to face an apparent paradox among the “hydrothermal community” species: a mollusk *Calyptogena magnifica*, the vestimentiferan *Riftia pachyptila*, and the crab *Bythograea thermydron* are present in both locations; others, such as the mytilid mussel, and the enteropneust, are restricted to the Galápagos Rift area (perhaps this reflects insufficient knowledge of the vent community at 21°N); the Alvinellinae form the only known example of speciation from a common ancestor resulting in 2 different species, one for each hydrothermal site. An explanation could be found in the different dispersal capabilities of the “hydrothermal community” components. It has been demonstrated, in the case of the new genus and species of Mytilidae from the Galápagos Rift, based on studies of the larval shell morphology of juvenile specimens, that these animals have a long planktonic larval life (Galápagos Biology Expedition Participants 1979; Lutz *et al.* 1980). Abyssal currents may transport the larval stage hundreds of kilometers. This is probably not the case with the Alvinellinae. In the family Ampharetidae, the few existing data on reproduction and larval development show that the eggs are usually deposited in the tube of the female, and that larval development is non-pelagic, larval stages beyond the 3-setiger stage being found outside the mother tube, on the mud surface. This has been observed for the Ampharetinae (Zottoli 1974), as well as for the Melinninae (Nyholm 1950).

Even the free benthic larval stage seems to be rather short, probably a few days or a few hours. For *Amphicteis floridus*, it has been shown in the laboratory that 3-setiger larvae begin tube-building just after leaving the tube of the female (Zottoli 1974). Dispersal capabilities thus appear very limited. On the other hand, biogeographical data show that several species of Ampharetidae, mainly from shallow waters, have a very wide distribution, for example *Amphicteis gunneri*, *Anobothrus gracilis*, *Ampharete acutifrons*, *Melinna cristata*. Even a truly deep-sea species such as *Amphicteis sargassoensis* Hartman and Fauchald has been found in the Atlantic Ocean from Walvis Ridge in the southeastern part to the northwestern part. In the present state of knowledge of the Alvinellinae, it seems that the following hypothesis can account for these two opposite sets of data: even with their very low dispersal capabilities, the genetic flow is sufficient to prevent rapid speciation when the physical environment constantly provides suitable conditions for life. The special physical environment provided by the hydrothermal activity is not likely to be constant; due to their strict and distinct adaptation to this environment the two species of Alvinellinae probably originated from a single ancestral population and were isolated over time into a series of sub-populations where speciation occurred independently. *Alvinella pompejana* and *P. grasslei* must be considered as two examples of this process, and one can expect other new taxa to be found in different locations where hydrothermal vents occur. This hypothesis leads to the following remark: at the present time, since the intermediate morphological types that could exist between the two known

species of Alvinellinae have not been found, it seems practical to establish two distinct genera, fully justified on the basis of conventional taxonomical criteria. It must be stressed that the generic criteria serving to differentiate *A. pompejana* and *P. grasslei* are the ones ordinarily used within the family Ampharetidae.

Résumé

A proximité immédiate des sources hydrothermales chaudes découvertes à l'est des îles Galapagos, ont été récoltés divers organismes animaux souvent inconnus et formant une communauté exubérante. Parmi eux, une Annélide polychète a été récoltée dans les amas de tubes de Vestimentifera. Cette Annélide appartient à une espèce nouvelle, *Paralvinella grasslei* gen. sp. nov., et doit être rangée dans la sous-famille des Alvinellinae récemment créée au sein des Ampharetidae pour renfermer *Alvinella pompejana* Desbruyères et Laubier, 1980, espèce récoltée sur un autre site hydrothermal de la ride du Pacifique oriental par 21°N. *Paralvinella grasslei* présente des adaptations moins marquées que celles de *A. pompejana*. Une comparaison entre ces deux formes est faite et une hypothèse sur leurs liens phylogénétiques est proposée.

Acknowledgments

We thank F. J. Grassle, Woods Hole Oceanographic Institution, for placing at our disposal the first specimen sorted from a sample studied by H. Sanders and Nancy Copley, M. H. Pettibone, Smithsonian Institution, for reviewing this manuscript, and M. L. Jones for sending us the second specimen and reviewing the paper. This is Contribution n° 25 from the Galápagos Rift Biology Expedition, supported by the National Science Foundation and Contribution n° 755 from the Centre Océanologique de Bretagne.

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